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昆虫个体大小对其种群生物学的影响

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摘要:个体大小是昆虫种群最直观的表型之一。很多研究发现,个体大小可对昆虫的许多生物学特性产生影响,由此影响昆虫种群的发展以及所在群落的结构和功能。根据最近 20 多年的相关文献,综述了个体大小对种群以下几方面的影响:成虫求偶、交配、生殖力及后代适合度,飞行及与飞行相关的其他行为如觅食、空中求偶和交配,摄食能力和食料种类,竞争和防御能力,抗逆性,以及社会性昆虫的劳动分工等。通常情况下,与同种内较小个体相比,较大的昆虫在生殖、飞行、抗逆性等方面往往具有优势,有助于种群适合度的提高。最后提出了几点可供此领域研究参考的建议和应用启示。

关键词:体形;昆虫;生殖;飞行;觅食;竞争;抗逆性;社会分工

Effects of body size on the population biology of insects

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Abstract: Body size is one of the most important life-history traits of insects. As demonstrated in numerous studies, insect body size can have substantial effects on a number of biological characters, which in turn may influence population development as well as community structure and functions. In this paper, based on the studies published in the past two decades, we reviewed the major findings in this field, and focused on the effects of body size on following traits: 1) courtship, mating, fecundity of females and males, and fitness of their offspring; 2) flight performance, and the relevant behaviors such as foraging, aerial courting and mating; 3) food-uptake capacity and the type of preferred diets; 4) competition and defense capacity; 5) resistance to environment stress; and 6) labor division in social insects. In most cases, larger individuals are superior to small ones in certain aspects, reproduction, flight and adaptation to adverse environments in particular, which subsequently favors the increase of population fitness. We presented some viewpoints as to future studies, such as taking more biological traits into consideration when evaluating associations between body size and insect reproduction, and paying more attention on the ecological results of body size variance at the community level. From the practical perspective, it is suggested to take body size into account when developing insect-pest control or beneficial-insect utilization strategies.

Key Words: body size; insects; reproduction; flight; foraging; competition; stress resistance; social division

个体大小是生物最基本也是最重要的表型之一,它与生物的生长、发育、生殖和存活密切相关,是影响种群发展潜力及群落结构与功能的重要因子[1-9]。昆虫纲作为动物界最大的一个纲,已经历至少 4 亿年的演化时间(指有翅昆虫,无翅亚纲的昆虫可能更长),期间很多种类发生了体形上的变异。最近几十年来,有关昆见

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虫个体大小变异及相关影响因子的报道屡见不鲜[10]。有关昆虫个体大小对种群生物学影响的报道也较多,但十分零散。

鉴于此,作者根据最近 20 多年的相关文献,综述了昆虫个体大小对其生殖、飞行、摄食、竞争、防御、抗逆性、社会分工等方面的影响(表 1),以期提高对此领域的认识。同时,由于有关个体大小的理论可为解释诸多生态学现象提供科学依据,并可用于指导改进益虫利用和害虫防控技术,故期望本文还能给予读者实践方面的启示。

表 1　昆虫个体大小对其生物学特性的影响

Table 1　Effects of body size on biological traits of insects

生物学指标 Biological traits	昆虫 Insects	影响或表现状况 Specific effects or outcomes	参考文献 References
雌虫生殖及后代适合度:			
雌虫生殖力	本文	大个体雌虫的生殖力较大	本文
	豆象 *Stator limbatus*(Horn)	与大个体雄虫交配可提高生殖力	[11]
配偶选择	玉米根萤叶甲 *Diabrotica virgifera virgifera* LeConte	大个体雌虫易被选作配偶	[12]
交配持续时间	玉米根萤叶甲 *D. virgifera virgifera*;北美玉米根叶甲 *Diabrotica barberi* Smith & Lawrence	大个体雌虫时间较长	[12-13]
交配不应期①	暗脉菜粉蝶 *Pieris napi* L.	随前一次交配的雄性配偶个体的增大而缩短	[14]
产卵频率	网襀 *Isoperla aizuana* Kohno	大个体较高	[15]
雌虫适合度	缺肘反颚茧蜂 *Aphaereta minuta* (Nees)	大个体较高	[16]
生殖资源的配置	13 个科的 40 种寄生蜂;缺肘反颚茧蜂 *Aphaereta genevensis* Fischer	小个体动用生殖资源的时间较早	[17-18]
卵粒大小	本文	大个体雌虫产的卵粒较大	本文
后代雌性比	菜蚜茧蜂 *Diaeretiella rapae*(M'Intosh)	与大个体雄虫交配可提高后代雌性比	[19]
后代存活	菜蚜茧蜂 *D. rapae*	配偶双方个体大均有利于后代存活	[19]
雄虫生殖及后代适合度:			
求偶、交配和竞争能力	本文	大个体雄虫占优势	本文
精巢大小和精子长度	赤眼蜂 *Trichogramma euproctidis* Girault;74 种蝶类	与雄虫个体大小正相关	[20-21]
射精量或精包重量	豆象 *S. limbatus*;20 种螽斯;北美玉米根叶甲 *D. barberi*	与雄虫个体大小正相关	[22-24]
有效精子数量	地中海实蝇 *Ceratitis capitata* (Wiedemann)	与雄虫个体大小正相关	[25]
精子竞争	暗脉菜粉蝶 *P. napi*	大个体雄虫较强	[14]
性信息素滴度及释放量	星灯蛾 *Utetheisa ornatrix*(L.);丽蝇蛹集金小蜂 *Nasonia vitripennis*(Walker)	大个体含量较高、释放量较大	[26-27]
交配持续时间	北美玉米根叶甲 *D. barberi*	小个体雄虫时间较长	[13]
交配次数	分舌蜂 *Colletes perforator* L.	大个体雄虫的次数较多	[28]
后代成虫的个体大小	美洲沙漠蝗 *Schistocerca americana* (Drury)	大个体雄虫的后代成虫个体较大	[29]
飞行及相关行为:			
翅形、翅脉、气孔和胸部肌肉	马蜂亚科 Polistinae 的 12 个属 56 个种	本文	[30]
飞行肌重量、后翅长	棱脊绿色螅 *Mnais costalis* Selys	大个体较重、较长	[31]

续表

生物学指标 Biological traits	昆虫 Insects	影响或表现状况 Specific effects or outcomes	参考文献 References
MLF 和 SCLF	棱脊绿色蟌 *M. costalis*	MLF 随体形增大而增大,SCLF 反之	[31]
眼的形态及其对光的敏感性	地熊蜂 *Bombus terrestris* L.、红尾蜂 *Bombus lapidarius* L.及另外一种熊蜂 *Bombus pascuorum*(Scopoli)	大个体眼的面直径大、小眼多、单眼大,对光较敏感	[32]
触角上嗅觉感受器的数量、密度及其对气味分子的敏感性	地熊蜂 *B. terrestris*	大个体较多、较高、较敏感	[33]
飞行距离或归巢能力	6 科(地蜂科、蜜蜂科、分舌蜂科、隧蜂科、切叶蜂科和准蜂科)的 62 种蜂;6 种壁蜂 *Osmia* spp.;绿丛螽斯 *Tettigonia viridissima* L.	大个体较强	[34-36]
觅食能力	地熊蜂 *B. terrestris*	大个体对花蜜的觅食能力较强	[37]
步长	班腹刺益蝽 *Podisus maculiventris*(Say)	大个体较远	[38]
传播植物种子的能力	新西兰大沙螽 *Deinacrida connectens* Ander	大个体较强	[39]
寄生蜂搜寻寄主的效率	缺肘反颚茧蜂 *A. minuta*;吉氏角头小蜂 *Dirhinus giffardii* Silvestri	大个体较强	[16,40]
寄主植物范围:			
寄主特异性	多种取食无花果 *Ficus* 的昆虫;北欧 105 种尺蠖科昆虫	个体较小的物种其寄主植物范围窄于个体较大者	[41-42]
竞争和防御能力:			
侵占同种个体蜂巢的能力	顶切叶蜂 *Megachile apicalis* Spinola	大雌虫较强	[43]
强心苷含量(一种防御物质)	宽肩叶甲 *Oreina gloriosa* F.	大个体雄虫中含量较高	[44]
寄主被寄生所需时间	科列马・阿布拉小蜂 *Aphidius colemani*(Viereck)	寄主(桃蚜)越大,其被寄生所需时间越长	[45]
血细胞对寄生物或病原物的包囊作用强弱	家蟋蟀 *Acheta domesticus*(L.);毛眼林蚁 *Formica exsecta* Nylander	大个体较强	[46-47]
引起寄主产生防御行为的可能性	豆柄瘤蚜茧蜂 *Lysiphlebus fabarum*(Marshall)	大个体蜂易引起寄主防御(蚜虫腹管产生分泌物)	[48]
抗逆性:			
耐饥力	茧蜂 *Asobara tabida*(Nees);堆土细胸蚁 *Leptothorax acervorum*(Fabricius);大仰蝽 *Notonecta maculata* Fabricius	大个体较强	[49-51]
	熊蜂 *Bombus impatiens* Cresson	小个体较强	[52]
耐寒力	堆土细胸蚁 *L. acervorum*;黑菌虫 *Alphitobius diaperinus* Panzer,	大个体较强	[50,53]
热交换、散热和低温下失重的速率	黑菌虫 *A. diaperinus*;幻紫斑蛱蝶 *Hypolimnas bolina*(L.)	小个体较快	[53-54]
升温速率,体温调节能力	毛跗黑条蜂 *Anthophora plumipes*(Pallas)	大个体较快、较强	[55]
抗干燥能力	非洲南部 7 种皮金龟科 Trogidae 甲虫	大个体较强	[56]

①交配不应期(Refractory Period):指前后两次交配的间隔时间

1 个体大小对昆虫生殖的影响

个体大小可影响昆虫生殖的许多方面,包括求偶、交配、生殖潜力等,而且还可对后代的发育和存活产生影响。

1.1 对雌虫生殖的影响

许多研究表明,在同种昆虫内,与个体较小的雌成虫相比,个体较大者具有许多生殖优势,如生殖力较高,

竞争配偶的能力较强,被雄虫选作配偶的概率较高,交配的持续时间较长,产卵频率较高等[12,20,49,57]。在鞘翅目、双翅目、膜翅目和直翅目的一些昆虫中,卵巢管数目可随个体的增大而增多[57]。鉴于与生殖的重要关系,个体大小可作为衡量雌虫生殖能力和适合度的一个重要指标。

在上述诸多影响中,最突出的表现在于个体较大的雌虫生殖力相对较高。这已发现于多种昆虫中,如地中海实蝇 *Ceratitis capitata* (Wiedemann)[25],甘蔗金龟 *Antitrogus parvulus* Britton[58],白蜡窄吉丁 *Agrilus planipennis* Fairmaire[59],豆象 *Stator limbatus* (Horn)[11],秋白尺蛾 *Epirrita autumnata* (Borkhausen)[60],斑点木蝶 *Pararge aegeria* (L.)[61],长索跳小蜂 *Anagyrus kamali* Moursi[62],赤眼蜂 *Trichogramma euproctidis* Girault[20],缺肘反颚茧蜂 *Aphaereta minuta* (Nees)[16],茧蜂 *Asobara tabida* (Nees)[49],顶切叶蜂 *Megachile apicalis* Spinola[43]。但同时,一些研究也表明大个体雌虫的生殖优势在某些情况下也可能变成劣势。这在玉米根萤叶甲 *Diabrotica virgifera virgifera* LeConte 中的发现较为典型:大个体雌虫虽然较易被雄虫选为配偶,并且交配时间较长,但与小个体雌虫相比,其与雄虫交配时较易被其他雄虫干扰而中止交配[12]。

个体大小还能影响雌虫对生殖资源的配置策略。这种现象主要发现于卵育型寄生蜂中:此类寄生蜂的卵子发生指数(Ovigeny Index,为雌虫羽化时体内成熟卵子的数量与潜在生殖力之比值)与个体大小负相关,即与个体较大的种类或者同种中个体较大者相比,个体较小的雌虫在发育过程中较早动用生殖资源,在羽化时卵巢内即有较高比例的成熟卵[17]。

除了与自身的生殖相关外,雌虫个体较大还可提高后代的适合度。在许多昆虫中发现,大个体雌虫所产的卵粒相对较大,如豆象 *S. limbatus*[11],赤眼蜂 *T. euproctidis*[20],缺肘反颚茧蜂 *A. minuta*[16],豆柄瘤蚜茧蜂 *Lysiphlebus fabarum* (Marshall)[48],顶切叶蜂[43]。较大卵粒可为后代的早期发育提供充足的营养物质,在此有利条件下,此类卵粒通常孵化较早、孵化率较高,后代发育较快、存活率较高、体形也相对较大[43,63-64]。但是,情况并非完全如此,例如,在豆柄瘤蚜茧蜂中,虽然个体较大的雌蜂产下的卵粒较大,但后代的个体未必较大,这是因为,作为蚜虫的一种内寄生蜂,其后代发育除了受卵粒营养条件影响外,更大程度上受蚜虫寄主的大小、质量等因素的制约[48]。另有研究表明,卵粒大小与雌虫个体大小的关系因种而异[65]。

1.2　对雄虫生殖的影响

雄虫个体大小可对其交配和生殖行为产生较大影响,在一些昆虫中甚至是决定交配能否成功的关键因素[66-67]。总体而言,个体较大的雄虫往往在求偶、交配及交配后的精子竞争等方面占有优势,这已发现于多种昆虫中,如色蟌 *Hetaerina americana* (Fabricius)[68],异痣蟌 *Ischnura graellsii* (Rambur)[69],蟋蟀 *Gryllus campestris* L.[70],沫蝉 *Cercopis sanguinolenta* (Scopoli)[71],豆象 *S. limbatus*[22],西印度甘薯象甲 *Euscepes postfasciatus* (Fairmaire)[66],桉天牛 *Phoracantha semipunctata* F.[72],道氏无垫蜂 *Amegilla dawsoni* Rayment[73],杀蝉泥蜂 *Sphecius speciosus* Drury[74]。而且,雌虫也更倾向于选择此类雄虫进行交配,以提高生殖适合度,产生较多或较大的后代[22,70,75]。雄虫个体大小对生殖的具体影响主要表现在以下两个方面:

(1)个体较大的雄虫生殖力较高,产生的精子数量多、个体大、活力强,具有较强的交配后竞争能力[20,22]。Wedell 对 20 种螽斯的体形研究发现,个体较大的雄虫在交配时射精量较大,由此增强精子竞争力,促使对雌虫体内低活性精子的取代,进而提高受精成功率[23]。Gage 在蝶类中发现,雄虫个体大小与所产生精子的长度呈正相关,而较长的精子鞭毛动力较强,游动较快,在精子竞争中占有优势[21]。这些优势在一妻多夫制的昆虫中十分突出:此类昆虫的雌成虫经常长时间持有多头雄虫的精子,至产卵时才受精,故精子间的竞争尤为激烈,在此情况下,大个体雄虫因能产生竞争力较强的精子而易在交配竞争中取胜[21,23]。

(2)个体较大的雄虫营养状况相对较好,在求偶或交配时能给雌虫提供相对较多、或较大、或营养更丰富的彩礼(Nuptial Gift),更具有求偶和交配上的优势[24]。许多雄虫在交配时通过精包将彩礼传递给雌虫,精包中除精子外还含有一些雄性附腺分泌物、营养物质或从环境中获得的一些化学物质[76-77]。这些精包物质中,有的能被雌虫用于卵子发育,成为卵的一部分,由此提高雌虫生殖力[23],有的则能抑制雌虫短时间内与其他雄虫发生再次交配[24]。此外,在少数昆虫中,有的精包物质还具有保护功能。例如,黄瓜十一星叶甲食根亚

种 *Diabrotica undecimpunctata howardi* Barber 的雄虫在葫芦上获得一种苦味的四环三萜化合物后,能通过交配将其传递给雌虫,此后该物质被结合在卵粒中,保护卵粒免受捕食[78]。又如,宽肩叶甲 *Oreina gloriosa* F.的雄虫能生成强心苷,此物质在个体较大的雄虫中浓度相对较高,能通过交配传递给雌虫,在雌虫及后代防御捕食性天敌的过程中起重要作用[44]。

此外,个体大小还可对雄虫的生殖产生其他方面的影响。例如,个体较大的雄虫求偶信息素含量相对较高,释放量较大,有利于搜索和发现配偶[26-27];交配次数较多[28]等。

需指出的是,个体较小的雄虫虽然在交配竞争和生殖力方面不占优势,但有可能通过其他途径对此进行弥补,例如增强寻找配偶的活力[79],求偶行为更为敏捷[68,80],延长交配的持续时间[13]等。

2 个体大小对飞行及相关行为的影响

在许多有翅昆虫中,个体大小与翅的形状和飞行肌发育状况存在密切关系,因此是影响昆虫飞行及与飞行相关的其他行为如觅食、空中求偶与交配等的一个重要因子[30-32]。

个体大小与飞行能力关系的一个典型例子发现于胡蜂(社会性昆虫)中。在新热带区,不同种类的胡蜂有着相似的捕食习性,均依赖飞行进行迁移,且个体大小差异很大,由于具备这些特点,此类昆虫十分适用于个体大小与飞行能力关系的研究。García 和 Sarmiento 分析了其中马蜂亚科 12 个属 56 个种 526 个个体的体形与翅形、胸部肌肉组织(为翅动力产生的主要来源)的关系,发现个体较小的种翅形相对较圆,翅脉较集中在近侧区,气孔较大,胸部肌肉所占比例较大;而个体较大的种则翅形较瘦长,翅脉较往远侧区伸长,气孔较小,胸部肌肉所占比例较小[30]。从空气动力学的角度来分析,这些结构特征体现了不同个体大小的昆虫在飞行上的适应性。具体而言,小个体蜂的圆形翅有利于增加翅的横切面,胸部肌肉增多有利于提高翅动力,两者均有助于小个体克服飞行中的强阻力这一核心问题;气孔增大则有助于虫体控制翅迎角,缓解风力作用下出现翅弯曲的现象。而对个体较大的蜂而言,翅瘦长有利于其进行更积极和高效的飞行,降低对飞行肌的依赖,从而有利于克服较大体重导致的举升力难题;翅脉往远侧区伸长有助于应对空气粘滞力,防止长翅在拍打过程中发生变形[30,81]。因此,不论是大个体还是小个体昆虫,它们均已进化形成许多有利于各自飞行的形态结构。

除了与上述翅形、飞行肌等方面相关外,个体大小与体温调节能力也有关,进而影响到飞行行为[55,82-83]。例如,在膜翅目昆虫中,个体较大者体温上升较快,维持体温的能力较强,有利于其更早、更频繁和更快地飞行[55,82]。

在个体大小对与飞行相关的其他行为的影响上,以觅食能力最为显著。对蜂类[34-35]、绿丛螽斯 *Tettigonia viridissima* L.[36]等昆虫的研究发现,个体大小和觅食距离之间存在一定的正相关性,个体越大,飞行距离越远,觅食范围越大,觅食效率越高。

有关个体大小通过影响昆虫飞行能力进而影响求偶、交配、捕食或防御能力的报道较少。现有研究表明,大个体和小个体在这些方面各具优势。例如,Samejima 和 Tsubaki 对棱脊绿色蟌 *Mnais costalis* Selys 研究发现,大个体雄虫的飞行肌重量较大,有利于提高最大举升力(Maximum Lifting Force,MLF,是衡量飞行能力的常用指标,在静止空气中,飞行动物为了控制空中运动需使其举升力超过自身体重),从而有利于交配过程中托举雌虫和应对空中其他雄虫的竞争;但另一方面,飞行肌重量与体重之比(Flight Muscle Ratio)的上升可导致其体形校正举升力(Size-Corrected Lifting Force,SCLF,为 MLF 与身体干重之比,是一个加速度指标,可反映飞行时的空中敏捷程度)下降,使飞行的敏捷度降低。相比之下,对小个体而言,虽然因 MLF 较低其飞行能力受到限制,但较大的 SCLF 有助于提高其对飞行的控制能力和空中加速度能力,由此获得较高的飞行敏捷度,增强潜行交配、空中获取配偶、躲避天敌捕食的能力[31]。

3 个体大小对摄食能力和食料种类的影响

有关昆虫个体大小影响摄食的研究大多集中在蚁类。对弓背蚁 *Camponotus mus*(Roger)工蚁的研究发

现,嗉囊的食物负载重量和摄食速率均与体重呈正相关[84]。摄食速率随个体的增大而提高的可能原因是,个体增大后,头部随之加宽,头部与摄食相关的一些生理结构参数如食窦容积、食道直径等均相应增大,摄食时头部相关肌肉收缩产生的食窦泵压力也得以增强[84-85]。与前述生殖、飞行等情况类似,小个体昆虫也会产生一些与取食相关的适合度补偿行为,如对黄粪蝇 *Scathophaga stercoraria*(L.)的研究表明,与大个体相比,虽然小个体摄食的速度较慢,但能更快达到饱腹状态,且其保持身体活力所需要的食物量也较小,故在权衡分配用于取食、寻找配偶的时间时显得更具优势(Time Budget Advantage),即小个体较倾向于减少取食时间来增加寻找配偶的时间,以此提高交配方面的适合度[86]。对大黾蝽 *Aquarius remigis*(Say)雄虫的研究也发现了同样的情况[87]。

个体大小在一定程度上决定着昆虫所能利用的食料种类[88]。例如,个体较大的弓背蚁适合于摄食粘度高的花蜜以及流速快的蜜腺;相比之下,小个体弓背蚁由于食道横截面较小,难以吸取粘度高的食物,而只适合摄食粘度低且流速慢的花蜜[89]。

4　个体大小对竞争和防御能力的影响

研究说明,大个体的昆虫在竞争食物、侵占或保卫领地、防御天敌等方面均表现出一定的优势[43,75,90]。对体内含有化学防御物质的昆虫种类而言,大个体也占据竞争优势。如在宽肩叶甲 *O. gloriosa* 中,与其攻击和防御能力相关的物质强心苷在个体较大的雄虫中含量较高,因此,大个体雄虫更具竞争优势,而且雌虫也倾向于选择个体较大的雄虫进行交配,以提高自身及后代防御捕食性天敌的能力[44]。

然而,个体较大者由于目标明显,容易招致天敌攻击,对天敌昆虫而言则易导致寄主或猎物产生防御反应。例如,Ameri 等发现黑豆蚜 *Aphis fabae* Scopoli 会根据其寄生蜂豆柄瘤蚜茧蜂的个体大小做出判断,当遇到较大的寄生蜂时其腹管会分泌较多的防御物质[48]。

5　个体大小对抗逆性的影响

总体而言,同种昆虫中大个体的抗逆性较强。例如,个体较大者体内储存的能量物质相对较多,故耐饥能力较强[49-51]。又如,大个体对不适环境温度的耐受能力也较强。大个体昆虫的相对表面积(表面积与体积之比)较小,热惯性较大,散热较慢,较能适应寒冷的气候条件,故越冬存活能力较强[90-91]。例如,Baranovska 和 Knapp 对步甲 *Anchomenus dorsalis*(Pontoppidan)研究发现,春季采集的冬后个体比上一年秋季采集的个体要大,其可能的原因是越冬期间大个体的存活率相对较高[8]。同理,个体较大的昆虫对高温的耐受力也相对较强[92]。

在资源数量有限或存在环境胁迫的条件下,同种内较大个体也有可能表现出生存劣势[3,10]。例如,Couvillon 和 Dornhaus 对熊蜂 *Bombus impatiens* Cresson 研究发现,大个体工蜂的耐饥能力不如小个体工蜂,其可能的原因是大个体工蜂由于体形较大,其维持机体基本生命活动的能量消耗相对较大[52]。Yasuda 和 Dixon 对二星瓢虫 *Adalia bipunctata*(L.)研究表明,当食物充足时,不同大小的雄虫交配能力无差异;而当食物供给有限时,大个体雄虫由于需要更多的能量来维持机体功能,它们将较多的时间和精力投入在取食等能量积累活动上而不是交配上,从而导致交配中的成功爬跨及交配次数下降[93]。除食物限制外,较大个体在高温胁迫下也可能增加死亡率。以云杉线小卷蛾 *Zeiraphera canadensis* Mut. & Free.为例,在适宜环境温度下,雌蛾寿命与体形大小呈正相关,但当环境温度较高时,大个体雌蛾的体温升高幅度显著大于小个体雌蛾,故高温胁迫下雌蛾寿命反而与体形大小呈负相关[94]。

6　个体大小与社会性昆虫劳动分工的关系

对社会性昆虫而言,成虫个体大小与劳动分工存在密切关系。例如,在熊蜂蜂群中,工蜂间的体形差异很大,大工蜂的体重为小工蜂的 10 倍之多,大者主要负责外出觅食,而小者则主要在蜂巢内负责哺育幼虫、清洁

巢室等工作[32-33,37,52]。较大个体的工蜂之所以更擅长于在外觅食,原因有[32,37,52]:①吸吮食物的相关器官(如舌)和肌肉较发达,口器较易伸至蜜腺,吸食花蜜的速度也较快,故在相同时间内能采回较多的花蜜;②视觉系统较敏感,更容易探寻到花朵:与小个体相比,大个体工蜂的眼较大,小眼数量较多,眼斑直径和面直径较大,故对光的敏感性较强,有利于在清晨、傍晚等弱光条件下飞行,能较早探寻到花蜜资源(且许多花在清晨会比其他时间段有更高的花蜜储存量),或者在其他昆虫不易发现的较暗区域探寻到花朵;③嗅觉系统较敏感,有利于探寻到花朵:表现为触角嗅觉感受器的数量较多,密度较大,对气味产生行为反应的阈值浓度较低;④能较好地调节体温以便在较低温度下觅食飞行:有的熊蜂其大个体甚至在环境温度接近冰点时仍能维持飞行所需的体温;⑤不易被捕食。小个体工蜂在分工上的优势尚未得到证实[52]。

对蜂群而言,其生长、繁殖和存活强烈依赖于对花蜜和花粉的不断摄取,上述大个体工蜂在相关生理结构及感觉系统敏感性上的突出优势,恰能满足要求,体现了此类昆虫在种群生物学方面的强大适应性。

7 小结与展望

在最近 20 多年中,人们对昆虫个体大小与种群生物学的关系进行了较多研究,明确了该性状与生殖、飞行、摄食、竞争、防御、抗逆性、社会分工等种群行为的基本关系(表 1)。总体而言,在同种昆虫内,体形较大的个体在许多方面占有优势,有助于提高种群适合度。其中最主要的发现是,个体较大时有助于提高雌虫的生殖力,以及雄虫求偶、交配及交配后精子竞争的能力。对其他方面影响的报道相对较少,具体表现因种而异。值得注意的是,尽管同种内较大个体具有许多生活史优势,但在资源有限或存在环境胁迫的情况下,大个体也有可能处于生存劣势。这说明在昆虫个体大小的进化过程中存在一定的稳定化选择(Stabilizing Selection)趋势,也解释了一些个体大小与昆虫适合度并不相关的现象。

今后,此领域许多方面的研究有待加强。例如,在考察个体大小的生态学效应时,有待更多地将多个性状进行综合研究。如在评价雄虫大小与生殖的关系时,需将交配次数、射精量、精子竞争力、交配持续时间、交配恢复时间等多个生殖指标同时进行考察。这是因为,不同大小的雄虫在这些方面各有千秋,个体较大者在与雌虫的交配成功率、交配次数方面占有优势,而个体较小者可能在单次交配的持续时间和射精量、受精成功率等方面占有优势,若仅考察其中一二个指标,结果会失之偏颇[95]。

又如,除了在种群水平的影响外,还需考察个体大小在群落水平上产生的影响。研究表明,个体大小可通过影响昆虫的种群动态、遗传结构和生活史而影响与其他物种之间的关系,如捕食、寄生、种子扩散和授粉等。此方面以蜂类最具代表性。作为植物最重要的传粉动物,蜂类的觅食距离能影响多种开花植物的两性生殖过程,从而对植物种群的遗传结构产生较大影响,这种影响对处于生境碎片里的植物尤为明显[34]。

近年来,出现了许多有关昆虫个体大小与其他性状进化关系的报道,如发育期长短[96],蝶类眼点(眼状斑纹,可用于阻止天敌捕食)[97],蚁巢等级制度[98]等。还有少数研究将个体大小作为考察外来入侵昆虫适应性和进化程度的一个指标[99-100]。这些研究有助于我们从进化角度理解个体大小形成的机制及相关生态学效应,丰富对此领域的认识。

在应用上,有关昆虫个体大小与种群生物学关系的理论知识,对益虫利用、害虫防治技术的研发或改进具有重要指导价值。例如,在人工繁养昆虫时,需首先明确环境条件对其个体大小的影响状况,以及个体大小对交配、生殖和后代适合度的影响,进而优化繁养条件,得到具最优个体大小的昆虫。在采用昆虫不育技术控制害虫时尤其需注意这一点,这是因为,此项技术的要点是尽可能提高释放的不育雄虫与野外雌虫的交配能力和授精能力,其中繁育出大小合适的雄虫是关键[66]。又如,在采用庇护所策略治理靶标昆虫对转基因作物的抗性时,需考虑到庇护所植物和转基因作物上靶标害虫的个体大小差异及其对相互间交配能力的影响;若两类植物上害虫个体大小差异明显,并由此影响到交配,则庇护所不能起到稀释抗性基因的作用[13,30,101]。在利用蜂类作为传粉昆虫来提高作物产量时,则需考虑其个体大小与飞行及归巢能力之间的关系,从而确定其最大可传粉范围[34-35]。

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